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What volume of seeds can a chimpanzee carry in its body?

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Abstract

Great apes are important seed dispersers with large bodies, able to swallow large seeds and travel long distances. Although there have been several studies investigating seed dispersal quality [sensu Schupp (Vegetatio 107/108:15–29, 1993)] by chimpanzees, there is little information on the volume of seeds they can carry in their bodies. When a relatively fresh corpse of a mature female chimpanzee was found at Mahale, Tanzania, we took advantage of the rare opportunity to investigate the total weight and cubic volume of seeds recovered from the corpse. The seeds contained in the corpse weighed 258.8 g (dry weight) and measured 489.4 cm^3. The volume of seeds was 14.7% of the previously reported capacity of the digestive tract of a chimpanzee in captivity. We also indirectly estimated the volume of seeds from the values of observed seed volume in feces, the reported number of defecations per day, and the seed passage time. The estimated volume was significantly lower than the observed seed volume, suggesting that the number of defecations per day is underestimated because it may not include nighttime defecation.

Keywords: Endozoochory, Mahale Mountains National Park, *Pan troglodytes*, Seed dispersal, Seed volume

Introduction

Frugivorous primates are important seed dispersers in several tropical forests (reviewed in Chapman 1995), and great apes are no exception to this. For example, apes may be more important seed dispersers for some plant species than non-ape primates, elephants, or frugivorous birds (Haurez et al. 2015). Sympatric cercopithecoid monkeys usually spit out seeds after processing them in their cheek pouches, whereas great apes typically swallow even large seeds and defecate them intact (Lambert 1999; Gross-Camp and Kaplin 2011). These two methods of seed dispersal may have different merits and functions. Cercopithecine monkeys disperse seeds via spitting, thus they do not fall very far from the parent tree. However, it is demonstrated that the removal of their adhesive pulp by teeth can result in high germination rates of these seeds (Lambert 2001). On the other hand, great apes tend to disperse seeds further from the parent tree, as they carry seeds in their digestive systems (Gross-Camp and Kaplin 2011). This may provide different opportunities for the dispersal of plant species which complements the shorter seed dispersal by monkeys. The larger body size of apes also has some merits—for

example, when fruit is so large that it precludes easy utilization by other animals, large-bodied great apes can sometimes be almost exclusive dispersers of their seeds (Tutin et al. 1991). Despite their lower densities in comparison with other primate species, great apes can contribute about half of the seeds dispersed through primate feces (Poulsen et al. 2001); this may also be due to their large body size. The total number of dispersed seeds does not directly relate to the success of these seeds because the ultimate success is largely determined by seed predation, removal, or fungus infection after dispersal (Lambert 2002a). Nevertheless, as far as primary seed dispersal is concerned, that by great apes can be characterized by longer dispersal distance and a large amount.

The chimpanzee (*Pan troglodytes*) is the most well-studied ape species, and there have been several studies regarding their seed dispersal. Such studies include investigations into the way chimpanzees process seeds (Lambert 1999; Gross-Camp and Kaplin 2011), the retention time of swallowed foods when chimpanzees are in captivity (Idani 1986; Lambert 2002b), the germinability of seeds that have passed through a chimpanzee's digestive tract (Takasaki 1983; Takasaki and Uehara 1984; Wrangham et al. 1994), the fates of the defecated seeds in natural settings (Gross-Camp and Kaplin 2005; Turner 2006; Dutton et al. 2014), and the relationship between the size and the shape of swallowed seeds (Nakamura and Itoh 2015). As regards two components of the effectiveness of seed dispersal defined by Schupp (1993)—quantity (i.e., the number of visits to the plant and the number of seeds dispersed) and quality (i.e., seed treatment and deposition)—most of these former studies focused on quality.

Compared to the quality of seed dispersal, there has been relatively less focus on quantity. Although chimpanzees are thought to disperse considerable volumes of seeds because they are highly frugivorous, there have been no reports on the quantity of seeds that they carry in their digestive tracts. There are largely two ways to estimate this: by directly investigating the stomach contents of a dead animal, and by indirectly calculating the estimated volume of seeds. For example, if we know the average volume of seeds in a fecal clump, the number of fecal clumps defecated per day, and the duration that a swallowed object stays in the digestive tract, we can calculate the volume of seeds in a chimpanzee's body.

To the best of our knowledge, there have been no studies reporting the stomach contents of wild chimpanzees. Although there are some earlier studies that examined the stomach contents of wild-shot primates [e.g., Fooden 1964; Izawa 1975 (both on New World monkeys)], they only reported what kinds of foods were in the stomach and there were no detailed descriptions of food quantity [however, Izawa (1975) specifically noted that there were 21 large seeds sized 27.5 mm in the stomach of *Lagothrix*]. It is no

longer ethically permissible to shoot primates merely to examine their stomach contents. Thus, in this study, we took advantage of a rare opportunity offered by the discovery of a relatively fresh corpse of a wild chimpanzee to investigate the species and the quantities of seeds in the dead chimpanzee's body. Because seed sizes differ depending on the plant species, the total number of seeds alone would have been insufficient for our general purpose. Therefore, by utilizing the previously published average seed sizes for plant species (Nakamura and Itoh 2015), we estimated the total volume of the seeds contained in the chimpanzee's body.

In addition, we indirectly estimated the volume of seeds in the chimpanzee's digestive tract using the number of seeds in chimpanzee fecal clumps, the average number of chimpanzee defecations per day, and the seed passage time (the latter two values were taken from the literature). We then compared this estimated volume with the volume of seeds actually observed from the dead chimpanzee.

Methods

The study was conducted in the Mahale Mountains National Park in Tanzania where a group of chimpanzees called the M group has been habituated and is the subject of a long-term study [see Nakamura et al. (2015) for details of the field site and the target group].

Seeds recovered from a dead chimpanzee's body

A dead female chimpanzee (adolescent or adult, judging from the body size) was found on 3 November 2013 by research assistants in the midst of the M group's exclusive home range. She might have died 1–3 days earlier. Because there was no identified female missing from the M group at that time, the dead female was assumed to be an unidentified immigrant which had recently joined the M group. Maggots were observed in the eye sockets but there were no injuries to the skin, indicating that the body was found before being scavenged. The body was sent to the park headquarters, refrigerated, and later autopsied by a national park veterinarian on 5 November 2013. The cause of death was assumed to be pneumonia. After the autopsy, the whole body was put into a large plastic sack and buried in the ground to decompose the soft tissue. On 28 May 2014, we recovered the whole skeleton and the seeds that remained in the plastic sack. We counted the number of these seeds for each species. We already knew the average length (the longest axis; L) and width (the second longest axis; W) for the majority of these species (Nakamura and Itoh 2015). For one species that was not listed in the previous study, we measured the corresponding sizes. Assuming that each seed approximates an ellipsoid of $L \times W \times W$, we calculated the volume of each seed. By

multiplying this figure by the number of seeds of each species, we estimated the total volume of seeds observed in the corpse (V_{obs}).

Indirect estimation from fecal clumps

We collected 41 fecal clumps at Mahale from September to December 2006, in a different year but in the identical food season to that during which the corpse was found. For each fecal clump, we identified the species and counted the numbers of seeds contained (except for tiny *Ficus* seeds). As mentioned above, we calculated the volume of each seed from the known average seed length and width of the species and calculated the total volume of seeds in each fecal clump (V_{feces}). Acting on a report that a Gombe chimpanzee defecates 6.7 times a day on average (Wrangham et al. 1994), we randomly extracted 6.7 fecal clumps from the 41 (in fact we extracted seven fecal clumps, and multiplied the seventh by 0.7) and summed the total V_{feces} of these randomly chosen 6.7 fecal clumps (i.e., the total volume of seeds defecated in a day; V_{day}). We used 31.5 h (Lambert 2002b) as the average passage time of a seed through a chimpanzee's digestive tract. Therefore, $V_{day} \times 31.5/24$ is the expected volume (V_{exp}) of whole seeds in a chimpanzee body. We iterated this procedure 10,000 times to obtain a distribution of V_{exp} and then compared the obtained distribution with V_{obs}.

Results

Seeds from the corpse

When we recovered the skeleton, the plastic sack was not torn and even small phalanges were recovered. Thus, we concluded that we had obtained all the seeds (except for tiny *Ficus* seeds) in the body without any loss. No seeds were broken or had germinated. In total, 806 seeds were found in the corpse (Table 1; Fig. 1). The total dry weight of these seeds was 258.8 g. We calculated V_{obs} as 489.4 cm^3 (Table 1).

Table 1 Summary of seeds recovered from a dead female chimpanzee at Mahale.

Species	Family	Number of seeds	Seed size (mm)	Estimated total volume (cm^3)
Pseudospondias microcarpa (A.Rich.) Engl.	Anacardiaceae	769	15.7 × 8.00[a]	403.8
Pycnanthus angolensis (Welw.) Warb.	Myristicaceae	30	24.0 × 14.5[a]	79.5
Saba comorensis (Bojer ex A.DC.) Pichon	Apocynaceae	6	19.1 × 9.97[a]	6.0
Keetia venosa (Oliv.) Bridson	Rubiaceae	1	6.05 × 5.85[b]	0.1
Total		806		489.4

[a] Length × width: average seed size for this species (data from Nakamura and Itoh 2015)

[b] Length × width: average seed size measured in this study

Indirect estimation from fecal clumps

We determined that each fecal clump contained an average of 43.2 seeds (range 0–108 seeds), and the average V_{feces} was 31.5 cm^3 (range 0–126.3 cm^3). A total of 30 among 41 fecal clumps contained *Pseudospondias* seeds, the species most commonly found in the corpse. When we ran the 10,000 simulations of random extraction, we got an average V_{exp} of 278.1 cm^3 (range 35.7–677.9 cm^3; Fig. 2). The average V_{exp} was significantly smaller than V_{obs} because there were only 182 occasions among these 10,000 trials in which V_{exp} was larger than V_{obs} (thus, $p = 0.0182$).

Fig. 1a–d All the seeds recovered from the body of a dead female chimpanzee at Mahale. **a** *Pseudospondias microcarpa*, **b** *Pycnanthus angolensis*, **c** *Keetia venosa*, **d** *Saba comorensis*

Discussion

The dead female chimpanzee's body contained 258.8 g of seeds (dry weight) with a volume of 489.4 cm^3. The dry weight is obviously an underestimate of the total burden in the digestive tract because a chimpanzee actually carries seeds when they are still wet (unfortunately, we do not have data on the wet weight). On the other hand, the cubic volume obtained in this study may have been slightly overestimated because the third diameter of a seed is slightly smaller than the second diameter. However, as most of the seeds swallowed by chimpanzees are capsule-shaped (see also Fig. 1), we assume the second and the third diameters did not differ extensively; thus, the overestimation might have been minimal. Obviously, we would have obtained a more accurate volume if we could have directly measured the cubic volume of the seeds. However, the limitations of measuring apparatus at the field site prevented us from doing so. Our measures (length, weight, and number) are the simplest ones, and almost all fieldworkers can duplicate them with ease.

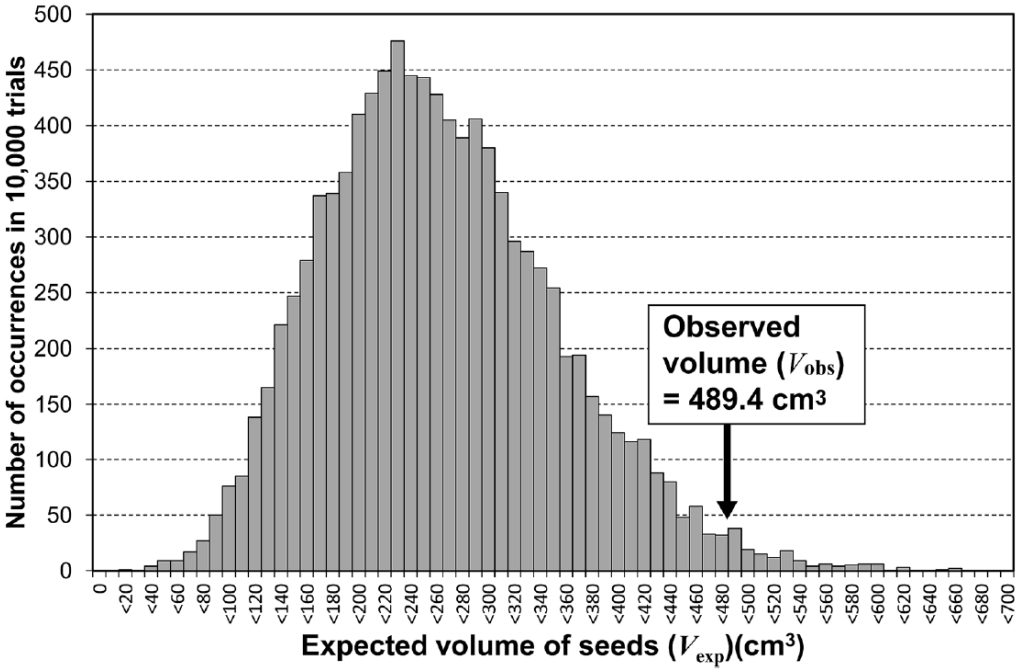

Fig. 2 Distribution of the expected volume of seeds (V_{exp}) calculated from 6.7 randomly selected fecal clumps. V_{obs} Total volume of seeds observed in the corpse

The total weight of the seeds is only 0.74% of the average female chimpanzee's body weight of 35.2 kg at Mahale (Uehara and Nishida 1987). Admitting that this is the dry weight of the seeds, and thus lower than the actual weight when in the chimpanzee's body, this small percentage might seem negligible; however, in terms of cubic volume, the seeds occupy 14.7% of the capacity of the digestive tract (stomach, small intestine, cecum, and large intestine), which was reported to be 3,322 cm^3 (965 cm^3 for the stomach alone) in a captive female chimpanzee (Chivers and Hladik 1980). This study is the first report to directly measure the quantity of seeds dispersed by a chimpanzee, although currently, it is difficult to judge how large a cost it was to the primate to fill 14.7% of its digestive tract with non-nutritional seeds.

V_{exp} from 10,000 simulations rarely exceeded the actual volume from the corpse (V_{obs}), and the average V_{exp} was about half the V_{obs}. These results suggest that one or some of the variables used to calculate V_{exp} may have been underestimated. The most likely candidate, we assume, is the number of defecations per day, which we derived from the literature (Wrangham et al. 1994). Although the study reporting this volume did not specify how this value was acquired, it is possible that this value represents defecations only during the daytime and does not include those at night. A recent study of nighttime behaviors of Mahale chimpanzees (Zamma 2014) revealed that they frequently defecate at night—even at midnight. If we calculate chimpanzee

defecations using V_{obs} and the average number of seeds contained in a fecal clump, the estimate is 11.8 defecations 24 h^{-1}. This suggests about five defecations during the night. Although we consider this to be a likely explanation, there are alternative explanations, of course. For example, if the female chimpanzee suffered from constipation before she died, this may have resulted in a larger number of seeds in her digestive tract than usual.

One should bear in mind that the volume of seeds reported in this paper is a value from a dead individual. The cause of death may influence the stomach contents. For example, in an extreme case, when the cause of death is starvation, the stomach of the dead chimpanzee is likely to be almost empty. Therefore, the value of seeds obtained from a dead individual may not necessarily represent that of healthy individuals. However, the value obtained from this study was even more than that estimated from known numbers of seeds from fecal clumps, suggesting that the dead chimpanzee might have eaten a normal amount of seeds or even more than normal before she died. Thus, it is unlikely that she died of starvation.

It is not common for researchers to find dead wild chimpanzees, particularly when corpses are still fresh and have not been scavenged. When we do find such corpses, we usually take some muscle samples for DNA analyses and skeletal samples for morphological investigation (Shimizu 2015). We suggest that researchers should also recover seeds from such dead bodies, when possible, to increase the sample size and to gain more accurate information on the cost to chimpanzees of carrying the seeds they disperse.

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